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Survival and growth of *Dendrobaena octaedra* (Savigny) in pine forest floor materials

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Summary. This laboratory study investigated the survival and growth of the epigeic earthworm *Dendrobaena octaedra* in pine forest floor materials. Moisture content is the major limiting factor for the survival of *D. octaedra*. L_2 material containing both herbaceous leaves as well as needles is the first decay stage in which significant growth of this worm species was observed. Maximum growth of *D. octaedra* occurred in F_2 material. Growth of *D. octaedra* may be affected by texture, microbial biomass and microbial community of the substrate. Decreased growth in H material previously worked by worms may have been due to a leachable growth-inhibiting compound.

Key words: *Dendrobaena octaedra*, earthworm growth, resource quality, pine forest floor

Introduction

Over the last few years the epigeic earthworm *Dendrobaena octaedra* (Savigny) has been invading forests in the Kananaskis Valley in SW Alberta, Canada (Dymond et al. 1996). Microcosm and field studies on the impacts of this species on the structure of the mor-type organic layers in *Pinus contorta* Loud. var *latifolia*. Engelm. forests have shown that, eventually, the entire F and H layers are replaced by worm casts.

D. octaedra grows well in pine F and H layer material (Dymond, Scheu & Parkinson, unpubl. data), but it is not known at which point in decomposition the litter becomes a suitable growth medium for *D. octaedra*. As pine needles decay, there are not only changes in their texture and moisture content but also in the associated microbiological (primarily fungal) communities. Earthworms have been shown to prefer softer leaves over harder leaves (Heath & Arnold 1966; Wright 1972), small organic particles over large organic particles (Judas 1992) and some fungi over others (Moody et al. 1995): Knowing this, it might be expected that earthworms would prefer the fragmented, microbially rich material in the F and H layers of the forest floor. However, it is known that other soil fauna do not necessarily grow best on the substrate they prefer (e.g. Klironomos et al. 1992; Shaw 1988).

The initial purposes of the present study were to determine first, the litter layer(s) or soil horizon(s) in which growth of *D. octaedra* was maximized; and, second, how soon after litterfall do pine needles become palatable to this species. However, questions arose from the results of this study which were investigated in two smaller studies on the factors affecting worm growth in L material and in H material previously worked by worms.

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3. Materials and Methods

Initial Experiment

Immature individuals (0.0031 to 0.1433 g) of *Dendrobaena octaedra* were heat extracted from lodgepole pine (*Pinus contorta*) forest floor material and kept at 5 °C in pine F/H material until needed. Samples of the lodgepole pine forest floor material were separated into L_1, L_2, F_1, F_2, H and H_w layers, and A_h and B_m horizons. The L_1 and L_2 materials used included leaves of grasses and herbaceous plants as well as pine needles.
Following sieving (4 mm), moisture contents of forest floor materials were determined and adjusted to optimum moisture content in an effort to eliminate the effect of moisture content. Soil layers used, their definitions, initial moisture and organic matter contents are given in Table 1.

Table 1. Forest floor substrates, their definitions, initial moisture content (48 h at 80 °C), and initial organic matter content (OM) (Loss on ignition at 400 °C (Nelson & Sommers 1982)) for the initial experiment

	Definition	Moisture content % fresh weight	% OM
L_1	light/medium brown, whole needles plus herbaceous leaves	60.9	98.4
L_2	dark brown, whole needles plus herbaceous leaves	83.0	96.9
F_1	black, non-fragmented needles → belongs to L	66.2	90.8
F_2	black, fragmented needles	67.4	77.3
H	black, amorphous organic material	65.3	67.9
H_w	black, amorphous organic material worked by worms	54.7	35.5
A_h	organic-rich mineral soil	48.2	33.3
B_m	mineral soil	16.8	5.3

This experiment was conducted in glass jars (6 by 5.5 cm diameter) with screw caps containing a hole which was plugged by cotton batting. Ten replicates of each of the litter and soil substrates were used. Each jar contained 1 cm depth of a substrate. One worm was added to each replicate of each substrate. Worms were gently washed in deionized water, blotted dry and weighed before addition to each jar. The jars were maintained at 15 °C during the experiment and worms were weighed every two weeks for eight weeks and returned to the jars after each weighing. The moisture content of the forest floor materials was adjusted to the initial moisture content after each weighing.

L Layer Experiment

In the initial experiment L_1 and L_2 layer materials contained a mixture of leaves and needles, therefore it was decided to investigate worm survival and growth in L_1 and L_2 material containing only pine needles.

Table 2. L layer pine needle substrates, their definitions, initial moisture content (48 h at 80 °C), and initial organic matter content (OM) (Loss on ignition at 400 °C (Nelson & Sommers 1982))

	Definition	Moisture content % fresh weight	% OM
L_1l_d	light brown, whole; dry	17.8	98.4
L_1l_m	light brown, whole; moist	26.4	98.4
L_1l_w	light brown, whole; wet	57.2	98.4
L_1m_d	medium brown, whole; dry	14.6	99.9
L_1m_m	medium brown, whole; moist	36.9	99.9
L_1m_w	medium brown, whole; wet	59.8	99.9
L_{2d}	dark brown, whole; dry	9.2	96.9
L_{2m}	dark brown, whole; moist	45.6	96.9
L_{2w}	dark brown, whole; wet	58.7	96.9

To clarify the effect of needles of differing early decay stages on growth of *D. octaedra* the L_1 material was separated into light brown, freshly fallen needles and medim brown needles which had been on the ground for several weeks. The L_2 needles had been on the ground for about eight months.
Because the L layers of the forest floor undergo considerable fluctuations in moisture content it was decided to investigate the survival and growth of *D. octaedra* at different moisture contents. The moisture contents of subsamples of each of the types of L material used were adjusted to approximately 10–20%, 30–40% and 50–60%. The L layer materials used, their definitions, initial moisture contents and organic matter contents are given in Table 2.
The experimental procedure for studying worm survival and growth was the same as that described for the initial experiment.

H Layer Experiment

Results from the initial experiment showed that survival and growth of *D. octaedra* were reduced in H material in which worms had previously been active (H_w) relative to H material which had not been exposed to worm activity (H). This experiment was designed to test the hypothesis that inhibition of worm growth in H material previously worked by worms was a result of the presence of a water-soluble compound in worm casts. Therefore in this experiment unleached H and H_w materials were used together with H and H_w materials which had been leached in deionized water. Preliminary experimentation had shown that 5 leachings with 100 ml deionized water per 20 g substrate decreased ammonium content in H and H_w material to the same low level. The H materials used, their definitions, initial moisture and organic matter contents are given in Table 3.

Table 3. Types of H layer materials used, their definitions, initial moisture content (48 h at 80 °C), and initial organic matter content (OM) (Loss on ignition at 400 °C (Nelson & Sommers 1982))

	Definition	Moisture content % fresh weight	% OM
H	black, amorphous organic material	70.9	67.9
Hl	black, amorphous organic material; leached	73.6	70.9
H_w	black, amorphous organic material; worm-worked	55.0	35.7
H_wl	black, amorphous organic material, worm-worked; leached	63.5	41.0

The experimental procedure for studying worm survival and growth was the same as that described for the initial experiment. However, after leaching and prior to the beginning of the experiment and at the end of the experiment, extractable ammonium and nitrate of the leached and unleached H and H_w substrates were assessed using Nesslerization and chromotropic acid methods, respectively (American Public Health Association 1971; Sims & Jackson 1971).

Statistical Analysis

Mortality of worms in each substrate was regressed against substrate moisture content and organic matter content. Worm growth was assessed as total growth during the experiment on a percent mass basis (((final wt-initial wt)/initial wt) × 100). Worm growth data for each substrate were regressed against substrate moisture content, organic matter content, and initial worm weight. Growth was significantly affected by initial worm weight and to remove this effect initial worm weight was used as a correlate in ANCOVA. Worm growth data in experiments 1 and 3 were log transformed to conform with the assumptions of ANOVA. Worm growth data for each substrate in the third experiment were also regressed against initial and final ammonium and nitrate concentration in each substrate.

Results

Initial Experiment

During the course of the experiment, 90% of the worms in the F_1 and a few of the worms in the F_2, H and A_h material matured (10%, 50% and 30% respectively). At the end of

the experiment all of the H and some of the F_1, A_h and B_m material had been converted into casts.

Mortality of *D. octaedra* was low in all but the B_m material (Table 4). Substrate moisture content explained 76% of the variation in mortality in all materials ($F = 25.55$, $p = 0.001$, $r^2 = 0.76$).

Growth of *D. octaedra* was significantly higher in the L_2, F_1, F_2, H and A_h layers than in the L_1, H_w, and B_m layers, and growth in the F_2 layer was significantly higher than in the L_2 and H layers (Table 4). Only 28% of the variation in worm growth could be explained by initial worm weight and substrate moisture content combined, of which 19% was due to initial worm weight ($F = 16.2$, $p = 0.0001$).

Table 4. Mean percent mortality and mean percent growth of *Dendrobaena octaedra* in forest floor substrates at the end of the initial experiment (i.e. after 8 weeks ($n = 10$). Values within columns followed by different letters are significantly different ($p < 0.05$)

	Mortality %	Growth %
L_1	10	1.5^c
L_2	0	415.6^b
F_1	0	450.7^{ab}
F_2	10	1125.0^a
H	0	386.8^b
H_w	20	-42.7^c
A_h	10	478.2^{ab}
B_m	40	-1.0^c

L Layer Experiment

In all types of L material at the lowest moisture content, all individuals of *D. octaedra* died (Table 5). Some individuals of *D. octaedra* survived in all types of L material at the highest moisture content but grew only in L_{2w} (Table 5). Substrate moisture content accounted for 68% of the variation in worm mortality ($F = 15.09$, $p = 0.006$, $r^2 = 0.64$).

Table 5. Mean percent mortality and mean percent growth of *Dendrobaena octaedra* in forest floor substrates at the end of the L layer experiment (i.e. after 8 weeks) ($n = 10$). Values within columns followed by different letters are significantly different ($p < 0.05$)

	Mortality %	Growth %
L_1l_d	100	–
L_1l_m	100	–
L_1l_w	70	-47.1^b
L_1m_d	100	–
L_1m_m	100	–
L_1m_w	10	-23.8^b
L_{2d}	100	–
L_{2m}	60	-20.8^b
L_{2w}	10	23.5^a

Worm growth in the four substrates in which *D. octaedra* survived was negative or very low. Initial worm weight and substrate organic matter content accounted for 34% ($F = 11.7$, $p = 0.002$) and 11% ($F = 4.8$, $p = 0.041$) of the observed variation in worm growth, respectively. There was no significant difference in growth of *D. octaedra* between L_1 material with or without leaves, however, in L_2 material the presence of leaves significantly increased growth of *D. octaedra* (Tables 4, 5).

H Layer Experiment

Mortality of *D. octaedra* was low in all treatments (Table 6). Growth of *D. octaedra* was not significantly different in the H, Hl and H_wl materials and was significantly higher in these materials than in the H_w (Table 6). Leaching of H_w significantly increased the growth of *D. octaedra*. Initial worm weight, substrate organic matter content and initial NO_3^- content accounted for 59% of the observed variation in worm growth, of which 27% was due to initial worm weight ($F = 13.9$, $p = 0.0006$).

Table 6. Mean percent mortality and mean percent growth of *Dendrobaena octaedra* in forest floor substrates at the end of the H layer experiment (i.e. after 8 weeks) ($n = 10$). Values within columns followed by different letters are significantly different ($p < 0.05$)

	Mortality %	Growth %
H	0	14.9^{a}
Hl	0	61.5^{a}
H_w	10	-48.9^{b}
H_wl	0	53.7^{a}

Discussion

Epigeic earthworm distribution has been correlated with soil moisture content (Phillipson et al. 1976). In the present experiment low moisture contents were associated with increased mortality of *D. octaedra* in both mineral and litter layers. In the litter layer this may relate to the bulk density of the litter material and hence the size of the pores. In L material, the needles and pores are large and the porespace relative humidity would be much lower than in A_h or B_m material of a lower moisture content. In L material, needle moisture contents below 46% were not sufficient to keep the worms alive, however 60% of worms survived in B_m material at 16.8% moisture content. In general, earthworms lose water rapidly at relative humidities less than 100% (Edwards & Lofty 1972; Lee 1985) although it is known that some species can survive water loss to about 60% of body weight (Roots 1956). Since mass movement by *D. octaedra* is thought to occur on the forest floor surface, and since the surface layers of the forest floor are the most susceptible to drying, the spread of this species will be limited in dry years.

Although initial worm weight accounted for 20 to 30% of the variation in growth of *D. octaedra* in each of the experiments, it was not sufficient to explain all the variation in growth observed. Characteristics of forest floor materials such as particle size/texture, microbial biomass and microbial community structure probably influenced growth of *D. octaedra*.

Particle size of organic substrates was an important factor determining growth of the endogeic earthworm *Aporrectodea caliginosa* (Boström & Lofs-Holmin 1986). However, there is evidence that endogeic worms ingest a higher proportion of small particles of amorphous and mineral material relative to epigeic worms which ingest a higher proportion

of larger, primarily organic, particles (Piearce 1978). Particle size probably did not account for the differences in growth of *D. octaedra* on different substrates in the present experiment since growth was not significantly different on L_2 and H materials, (i.e. whole or large pieces of needles and leaves, and amorphous organic material, respectively).

Food particles not small enough to be ingested whole must be chewed. Since during decay, tensile strength of pine needles decreases (Kendrick 1959), one would expect that worms would prefer more decomposed materials with low tensile strength such as those in the F and H layers. *Lumbricus terrestris* has been shown to prefer softened leaves regardless of their phenolic content (Wright 1972). In another study, palatability of leaf litters to *L. terrestris* was not affected by leaf penetrability or leaf or cuticle thickness (Satchell & Lowe 1967) but leaf penetrability was clearly much higher for deciduous leaves than for pine needles. In L material without herbaceous leaves in the present study, *D. octaedra* was observed grazing on the needle fascicles, which were probably much softer than the needles, but the worms did not grow very well on these substrates. The presence of herbaceous leaves in L_2 material significantly improved worm growth relative to that in other types of L material which may be partly due to the improved texture of the substrate.

The presence of fungi or bacteria has been shown to improve the palatability of leaves and paper discs to *L. terrestris* (Cooke 1983; Wright 1972) and the amount of fungus was positively correlated with worm preference (Cooke 1983). Fungal biomass, which represents c. 80% of the total microbial biomass in the pine forest floor, may be an important factor affecting worm growth in the present study. If this is true, and knowing that maximum fungal biomass tends to occur in the F layer (Visser & Parkinson 1975; Kjøller & Struwe 1982), then one would expect maximum worm growth to occur in F material, which was observed in the present study.

Differences in fungal or total microbial biomass between L_2 material which included herbaceous leaves as well as needles, and other L materials may account for the increased worm growth in the former material. This is supported by the fact that in nearby forests, fungal hyphal length in deciduous L_2 material exceeded that in L_1 material (Visser & Parkinson 1975).

While it is known form laboratory studies that soil mesofauna do prefer and survive and grow better on certain microbial taxa (e.g. Klironomous et al. 1992; Booth & Anderson 1979; Luxton 1972), and that earthworms do prefer some fungal taxa over others (Cooke 1983; Moody et al. 1995), it is not known whether earthworms require certain microbial taxa for optimum growth or whether they feed selectively in the field. Although we know that as pine needle litter decays the fungal community changes (Kendrick & Burgers 1962; Widden & Parkinson 1973), it is not known how important these changes may have been in affecting the growth f *D. octaedra* in different forest floor materials.

The significant decrease in growth of *D. octaedra* in H material previously worked by worms relative to H material unworked by worms may be due to a reduction in food quality of the substrate, to the buildup of a toxic nitrogenous compound(s) or to the buildup of some other growth inhibiting compound(s).

Decreased food quality in the H material is unlikely to be the cause of the observed decrease in growth since growth of *D. octaedra* significantly increased in leached H_w material.

Earthworm activity is known to add relatively large amounts of N to the soil through casts, urine, mucoproteins and in dead earthworm tissue largely as mineral N (Lee 1985). Nitrogenous compounds can be toxic to soil biota (Huhta et al. 1983; Marshall 1974) and it possible that some toxic nitrogeneous compound(s) accumulated in H material previously worked by worms. While the methods used in the present experiment to assess substrate ammonium and nitrate content were relatively crude, the results suggest that the significant decrease in growth of *D. octaedra* in H material previously worked by worms is not related to substrate ammonium or nitrate content.

It is suggested therefore, that some other leachable growth-inhibiting compound(s) is responsible for the observed decrease in growth in H material previously worked by worms.

Conclusions

In this forest floor material the prime limiting factor to survival of *D. octaedra* appears to be moisture content. This may limit the spread of this species in dry years.

L_2 material which included herbaceous leaves as well as pine needles was the earliest decay stage in which significant growth of *D. octaedra* was observed. In the absence of herbaceous leaves a small growth increase was recorded for *D. octaedra* in L_2 material but the F_1 layer was the earliest decay stage in which significant growth occurred. F_2 material promoted the highest growth of *D. octaedra*.

Growth of this species may be affected by substrate characteristics such as texture, microbial biomass and microbial community. In H material previously worked by worms, decreased growth may have been due to a leachable growth-inhibiting compound.

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